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Mackenziurus, a New Genus of the Silurian "*Encrinurus*" *variolaris* Plexus (Trilobita)

GREGORY D. EDGECOMBE¹ AND BRIAN D. E. CHATTERTON²

ABSTRACT

Mackenziurus reimeri n. gen. n. sp., from Wenlock strata in the Mackenzie Mountains, Northwest Territories, Canada, is designated type species of a new genus of the "*Encrinurus*" *variolaris* plexus. *Mackenziurus* n. gen. also includes Wenlock species from Wisconsin-Illinois and Arkansas. A sister-group relationship with *Fragiscutum* Whittington and Campbell is suggested; more recent

common ancestry with *Balizoma* Holloway is a competing hypothesis. Paraphyletic "*Nucleurus*" Ramsköld groups the sister taxa of *Balizoma*, *Mackenziurus* + *Fragiscutum*, and *Frammia* Holte-dahl. A silicified growth series for *Mackenziurus reimeri* provides new data on ontogenetic transformations for the *variolaris* plexus.

INTRODUCTION

The systematics of Silurian encrinurine trilobites were set in an explicit genealogical framework by Strusz (1980) who distinguished three "phylogenetic plexi" within *Encrinurus* Emmerich, 1844. Ramsköld's (1986a) subgeneric revision of *Encrinurus* formalized these relationships: *E. (Encrinurus)* and *E. (Pacifcurus)* Ramsköld, 1986b, comprise the Euramerican *punctatus* and Australasian *mitchelli* plexi, respectively,

whereas *E. (Nucleurus)* Ramsköld, 1986a, represents the plesiomorphic Llandovery core of the *variolaris* plexus. The latter group was envisioned as ancestral to restricted Wenlock?–Ludlow offshoots (*Fragiscutum* Whittington and Campbell, 1967; *Frammia* Holte-dahl, 1914) as well as to geographically widespread and morphologically conservative Wenlock–Ludlow *Balizoma* Holloway, 1980.

¹ Graduate student, Department of Invertebrates, American Museum of Natural History; and Department of Geological Sciences, Columbia University.

² Professor, Department of Geology, University of Alberta, Edmonton, Alberta, Canada T6G 2E3.

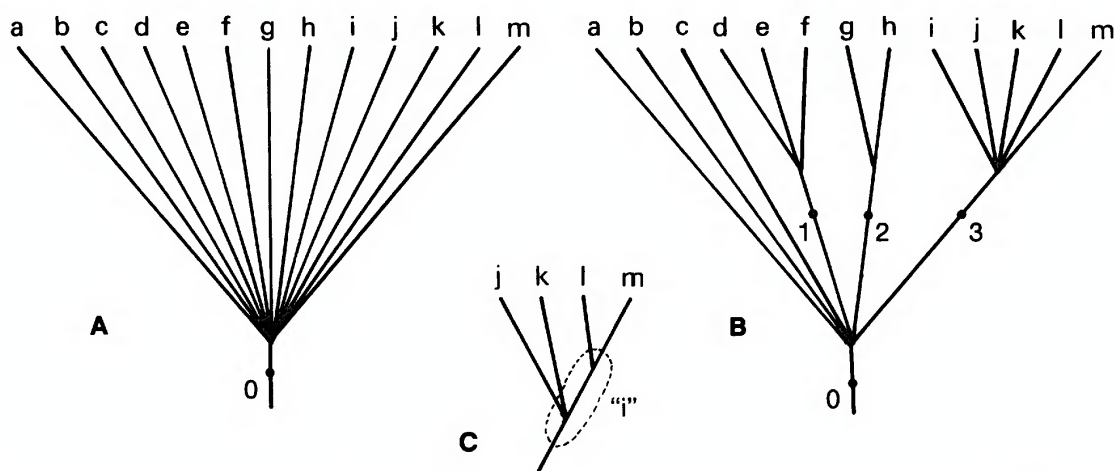


Fig. 1. Cladograms expressing component information retrieved from encrinurine classification (components analysis as outlined by Nelson and Platnick, 1981). A. Derivative cladogram from unsequenced generic list classification (Strusz, 1980: 8; cf. Hamada, 1961; Evitt and Tripp, 1977) predicts no component information additional to general component 0 (Encrinurinae). B. Cladogram expressing hypothesis of phylogenetic relationship for the same terminal taxa (from Strusz, 1980: fig. 9) is more informative, predicting three components. Unresolved polytomies within components 0, 1, and 3 result partly from paraphyletic ancestral taxa (0—*Encrinuroides*; 1—*Coronocephalus*; 3—*Encrinurus*; see C for example). C. Hypothesis of relationships between terms of component 3 (from Strusz, 1980: fig. 9); *Encrinurus* ("i") is paraphyletic. Terminal taxa abbreviated as follows: a, *Encrinuroides*; b, *Physemataspis*; c, *Cromus*; d, *Coronocephalus*; e, *Kailia*; f, *Senticucullus*; g, *Erratencrinurus*; h, *Celtencrinurus*; i, *Encrinurus*; j, *Paraencrinurus*; k, *Batocara*; l, *Fragiscutum*; m, *Frammia*.

The present survey offers an assessment of *variolaris* plexus relationships and taxonomy incorporating methods of phylogenetic systematics. We have thus attempted to recognize monophyletic taxa (*sensu* Hennig, 1966) based on synapomorphies, and to integrate these components into the hierarchical structure of classification. The information content (Mickeyvich and Platnick, 1989) of current encrinurine classifications is adversely affected by paraphyletic ancestral taxa (see fig. 1). A distinctive cluster of North American Wenlock species of the *variolaris* plexus is herein recognized as a monophyletic taxon and are described as the new genus *Mackenziurus*, with type species *M. reimeri* n. sp., from the Wenlock of the Mackenzie Mountains, Northwest Territories, Canada. Certain Wenlock species from Illinois, Wisconsin, and Arkansas previously referred to *Encrinurus* and *Balizoma* are reassigned to *Mackenziurus* n. gen. Type and figured specimens of *Mackenziurus reimeri* are housed in the paleontological type collections of the University of Alberta (UA).

Terminology applied to encrinurine morphology follows Evitt and Tripp (1977), with the exception that the conventional "axis" is used rather than "rachis." Description of encrinurine early ontogeny is as outlined by Edgecombe et al. (1988). The preglabellar lateral lobe is termed PL following Howells (1982), and description of glabellar furrows/lobes is as recommended for the revision of the Treatise on Invertebrate Paleontology, Part O (H. B. Whittington and S. R. A. Kelly, unpubl.). Ramsköld's (1986a) notations for fixigenal "circumocular tubercles" and terminal pygidial pleural ribs, as well as pygidial "R/P ratio," are adopted. "Major row" and "inter-row" glabellar tubercles are as introduced by Edgecombe and Chatterton (1987). Orientations use the typical abbreviations for sagittal (sag.), exsagittal (exsag.), and transverse (tr.).

ACKNOWLEDGMENTS

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SYSTEMATICS OF THE *VARIOLARIS* PLEXUS

Strusz's (1980) *Encrinurus variolaris* plexus included species referred by Ramsköld (1986a) to *Encrinurus* (*Nucleurus*) and *Balizoma* Holloway. *Fragiscutum* and *Frammia* were perceived as "offshoots," i.e., descendants excluded from the plexus. This distinction between ancestral and descendant taxa (Haeckelian ancestry of Rieppel, 1988) is not endorsed here; the *variolaris* plexus is expanded to include all descendants of a unique common ancestor which would itself be part of the group. "*Nucleurus*," *Balizoma*, *Fragiscutum*, *Mackenziurus* n. gen., and *Frammia* inclusively form a monophyletic group for which the informal name "*variolaris* plexus" is retained. Restricting this group to an ancestral/primitive core (e.g., "*Nucleurus*," with or without *Balizoma*) but excluding *Frammia* and *Fragiscutum* (based on their uniquely derived characters) results in a paraphyletic group. Schrank's (1972) synonymy of *Fragiscutum* and Reed's (1928) *Encrinurus variolaris* group with *Frammia* would eliminate several generic names widely used by subsequent workers. It seems most informative to retain existing names for expressing relationships between parts of the more inclusive *variolaris* plexus.

Characteristic of the *variolaris* plexus are reduction of L1 by adaxial merging of S1 with the occipital furrow, a forwardly positioned I-1 tubercle pair, a relatively broad glabella,

and an adaxially narrowing cranial anterior border. Although the usefulness of "a *variolaris* group" has been questioned on phenetic grounds (Temple and Tripp, 1979), monophyly of the *variolaris* plexus is supported by these unique characters; we hold that monophyly is both a necessary and sufficient criterion for a taxon's utility.

Enlarged L2-L4 lateral glabellar and adaxial fixigenal tuberculation, and reduced genal spines, are derived characters uniting this plexus with *Pacificurus* Ramsköld. It must be noted, however, that the occurrence of these states in certain Llandovery species with several diagnostic characters of the *punctatus* plexus (e.g., *E. squarrosus* Howells, 1982) cautions that they may be symplesiomorphies, and thus specify a more inclusive group (*Encrinurus* sensu Ramsköld, 1986a). (That hypothesis would demand reversals in derived parts of the *punctatus* plexus.) Predicting the component *variolaris* plexus + *Pacificurus* at the exclusion of the *punctatus* plexus, *Encrinurus* (cf. Strusz, 1980: 54), questions the grouping of *Encrinurus*, *Pacificurus*, and "*Nucleurus*" as a unique taxon (i.e., as subgenera of *Encrinurus*). Although that grade group might reflect the equivocal relationships of certain Llandovery species, it predicts that "*Nucleurus*" shares independent history with *Pacificurus* and *Encrinurus* rather than with other parts of the *variolaris* plexus. This statement [as retrieved from the classification; derivative cladogram (Nelson and Platnick, 1981) in fig. 2a] is incongruent with the phylogenetic hypothesis endorsed by Ramsköld (1986a) and herein that "*Nucleurus*" is most closely related to other genera of the *variolaris* plexus (fundamental cladogram in fig. 2b). Following Ramsköld's (1986a) diagnoses, *Encrinurus* (the *punctatus* plexus) and *Pacificurus* are treated as separate generic taxa herein to eliminate the paraphyletic "*Encrinurus*" created by grouping them with plesiomorphic parts of the *variolaris* plexus (the "*Nucleurus*" grade). This problem of paraphyly is only compounded when we entertain excluded (autapomorphic) sister groups for the other "subgenera" of *Encrinurus*. For example, "*E.*" (*Encrinurus*) is held to share most recent common ancestry with *Distyrax* Lane, 1988 (Edgecombe and Chatterton, in prep.), while monotypic *Batocara*

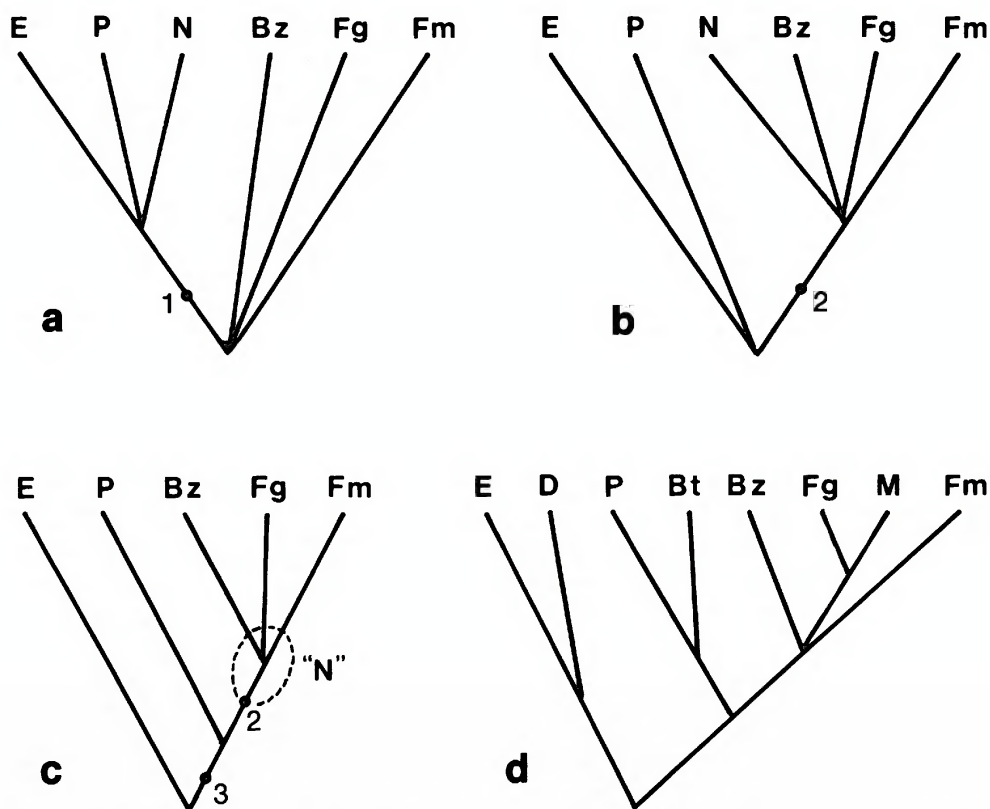


Fig. 2. Cladograms expressing alternative hypotheses of relationships for the *variolaris* plexus and allied taxa. Terminal taxa are abbreviated as follows: Bz, *Balizoma*; Bt, *Batocara*; D, *Distyrax*; E, *Encrinurus*; Fg, *Fragiscutum*; Fm, *Frammia*; M, *Mackenziurus*; N, *Nucleurus*; P, *Pacificurus*. **a.** Component information retrieved from Ramsköld's (1986a) classification; component 1 is *Encrinurus* (with three subgenera). **b.** Hypothesis of phylogenetic relationships, after Ramsköld (1986a); component 1 in the derivative cladogram a (fig. 2a) is incongruent with component 2 (*variolaris* plexus) in this fundamental cladogram. **c.** Hypothesis of relationships discussed herein; both components are congruent with cladogram b; *Nucleurus* is paraphyletic. **d.** Hypothesis of relationships including new (*Distyrax* Lane, 1988; *Mackenziurus* n. gen.) and previously excluded (*Batocara* Strusz, 1980) taxa.

Strusz, 1980, is interpreted as sister group to *Pacificurus* (if not part of the ingroup) (see fig. 2d). *Pacificurus* and Australian Ludlow *Batocara bowringi* (Foerste, 1888) share apomorphic hypostomal characters [long, triangular posterior border and conical rhynchos, e.g., *P. mitchelli* (Foerste, 1888)] and an enlarged pygidium. Similarities to particular *Pacificurus* species [e.g., coarse tuberculation as in *P. silverdalensis* (Etheridge and Mitchell, 1916); constricted glabellar stalk as in *P. rothwellae* (Etheridge and Mitchell, 1916)] are noteworthy.

The systematics of species assigned by Ramsköld (1986a) to *Nucleurus* are problematic, in part because many are inadequately

known. The diagnostic characters of "*Nucleurus*" are primitive for the more inclusive *variolaris* plexus as recognized herein; they are either shared with outgroups (e.g., *Pacificurus*, *Encrinurus*) or approximate the state at the outgroup node more closely than do other genera of the *variolaris* plexus. It is thus inferred that assigned species are more closely related to excluded genera than all are to each other. Revision of this paraphyletic group must search for monophyletic ingroup components and reassign other species to the "descendant" genus with which they share apomorphies.

The name *Nucleurus* remains available for a monophyletic group including the desig-

nated type species, *Nucleurus abyssalis* (Männil, 1977; see Ramsköld and Bassett, 1990, for revision). Morris (1988), however, synonymized *Nucleurus* and *Aristobeggia* Lamont, 1978 (type species *A. bargainensis* Lamont, 1978) with *Trippia* Lamont, 1978 (type species *T. penkillensis* Lamont, 1978). This action was based on Howells' (1982) synonymy of *T. penkillensis* and *A. bargainensis* with *Encrinurus mullochensis* Reed, 1931, a species which Ramsköld (1986a) referred to *Nucleurus*. Morris thus accepted the validity of Lamont's taxa, although Howells (1982: 27) did not. While Howells' synonymy of *T. penkillensis* appears plausible (although not certain until Lamont's types are identified), the paraphyletic composition of "*Nucleurus*" sensu Ramsköld (1986a) renders the simple substitution of *Trippia* inadequate. Pending revision of equivocal species, "*Nucleurus*" is used throughout the following parts of this paper as a paraphyletic grouping of primitive parts of the *variolaris* plexus.

SYSTEMATIC PALEONTOLOGY

FAMILY ENCRINURIDAE ANGELIN, 1854

SUBFAMILY ENCRINURINAE ANGELIN, 1854

MACKENZIURUS N. GEN.

TYPE SPECIES: *Mackenziurus reimeri* n. gen. n. sp. from the Delorme Formation (Wenlock), approximately 10 km east of Avalanche Lake, Mackenzie Mountains, Northwest Territories, Canada.

OTHER SPECIES: *Encrinurus* sp. of Tripp et al., 1977, from the Middle Wenlock of Illinois and Wisconsin; *Balizoma* sp. of Holloway, 1980, from the Wenlock of Arkansas. The specific name *Encrinurus laurige*, referred to Tripp et al. (1977) by Emielity and Bradbury (1986) for Niagaran material from Brookfield, Wisconsin, is a nomen nudum based on the species left in open nomenclature by Tripp et al. (1977). This species of *Mackenziurus* will be formally diagnosed in a forthcoming work by K. C. Gass, G. D. Edgecombe, and L. Ramsköld.

DIAGNOSIS: Genus of the *variolaris* plexus of relatively small size. Librigenal field subequal in length (exsag.) and height (tr.) to precranial lobe, with a row of about six coarse tubercles. Hypostome with inflated but me-

dially flattened middle body of subcircular outline; broad rhynchos and maculae inconspicuous; posterior border short. Pygidium subhemispherical in outline, with 6–8 pairs of pleural ribs and 7–9 axial rings (R/P ratio 1.1–1.3); sagittal groove narrow; coarse sagittal tubercles typically present on every second ring; inner margin of doublure with posteromedian notch broad and shallow or lacking.

ETYMOLOGY: Mackenzie, and Greek *oura*, tail; referring to the Mackenzie Mountains, where the type species occurs.

DISCUSSION: *Mackenziurus* n. gen. comprises a morphologically distinctive, temporally and geographically restricted clade within the *variolaris* plexus. Uniquely diagnosing the genus requires that several cephalic characters of *Mackenziurus* sp. (Tripp et al., 1977) are identified as plesiomorphies (i.e., shared with each of the outgroups "*Nucleurus*," *Fragiscutum*, and *Balizoma*); these serve to emphasize the many autapomorphies of *M. reimeri* n. sp. The type species differs from the Wisconsin-Illinois taxon in its broad rostral plate and frontal glabellar lobe, enlarged adaxial fixigenal tubercles opposite S1–S2 in large holaspides, and exsagittally aligned L4 tubercle pair (other specific differences are noted below in discussion of *M. reimeri*). *Mackenziurus* sp. (Tripp et al.) has a more gradually widening glabella (MPM 26515, figured by Tripp et al., is distorted), four subequal-sized fixigenal tubercles overhanging the axial furrow, and apparently a typical *variolaris* plexus wedge-shaped/narrow trapezoidal rostral plate. The well-rounded cranial anterior margin (versus the medially flattened margin of *M. reimeri* n. sp.) suggests that the anterior margin of the hypostome is probably rounded and less pentagonal in outline than is that of the type species. These plesiomorphies, however, provide no evidence that either *Mackenziurus* species should be grouped with another genus of the *variolaris* plexus rather than with each other.

It might be argued that the distinctive autapomorphies of *M. reimeri* could warrant the erection of a monotypic genus, whereas *Mackenziurus* sp. (Tripp et al.) could be retained in *Balizoma* or some "ancestral taxon" based on symplesiomorphy. This has

been avoided to minimize paraphyly and redundancy (monotypy). It is more informative to broaden the diagnosis of *Mackenziurus* (i.e., exclude the unique specific characters of *M. reimeri*) to recognize a more inclusive monophyletic group indicated most clearly by pygidial synapomorphies. The diagnostic characters of *Mackenziurus* predict that *M. reimeri*, *Mackenziurus* sp. (Tripp et al.), and (most doubtfully, due to missing data) *Mackenziurus* sp. (Holloway) are each other's closest relatives, sharing common ancestry excluding all other encrinurines of the *variolaris* plexus. Priority is placed on identifying monophyletic groups, rather than speculating on whether or not a species group is distinctive enough to warrant generic ranking. Our rationale for erecting a new taxon (at the generic level by convention) is thus to identify a monophyletic group and discuss its historical relations to other taxa. If the evidential (i.e., character) support for grouping *Mackenziurus* species is judged insubstantial, we would caution that the alternative (a lack of any evidence for grouping each species with different clades) is surely more suspect.

The search for *Mackenziurus*' sister group within the *variolaris* plexus reveals conflicting character distributions, different characters suggesting closest relations to either *Fragiscutum* or *Balizoma*. It is noted, however, that identifying *Mackenziurus* as a hypothesized monophyletic group does not appear to render any existing genus paraphyletic (e.g., species of *Balizoma* sensu Ramsköld, 1986a, share more unique characters among themselves than with *Mackenziurus*).

Mackenziurus is particularly comparable to *Fragiscutum* in the following characters:

1. Nonenlargement of PL relative to adaxial tubercles on the cranial anterior border. Strusz (1980: 39) cited this character as diagnostic of *Fragiscutum* (in contrast to most "Nucleurus" and *Balizoma* spp. with enlarged PL), but it is more general (shared with *Mackenziurus*);

2. reduced number of tubercles in the adaxial fixigenal tubercle row (see discussion below);

3. rounded, medially flattened hypostomal middle body. This similarity between *F. glebale* Campbell, 1967, and *M. reimeri* (but also juvenile *F. rhytium* Whittington and

Campbell, 1967) forces a homoplasy; either this resemblance is convergent, or *F. rhytium*'s more general (*Balizoma*/"Nucleurus"-like) adult form is a reversal (both transformations are equally parsimonious);

4. inconspicuous maculae;

5. low field of the librigena. *Mackenziurus reimeri* and *Mackenziurus* sp. (Tripp et al.) have a librigenal field about 70 percent as high (tr.) as the lateral border (measured beneath the eye), *Fragiscutum* has 50–60 percent. Although some Ludlow *Balizoma* species have a comparably low genal field [*B. obtusa* (Angelin, 1851); specimens figured by Schrank (1972) and Ramsköld (1986a)], this is interpreted as a convergent similarity to *Mackenziurus* (and *Fragiscutum*), since it does not appear to be the plesiomorphic condition for *Balizoma*. Wenlock *B. variolaris* (Brongniart, 1822) (see Tripp et al., 1977) has a librigenal field taller than the lateral border, as does Ludlow *B. hyperborea* (Thomas in Thomas and Narbonne, 1979). Wenlock taxa of the group most closely allied to *B. obtusa* [following Ramsköld's (1986a) species synonymy] have a taller genal field than Gotland Ludlow samples; northern Canadian specimens figured by Perry and Chatterton (1977, 1979, and unpubl.) have a field about 85 percent as high as the lateral border. Accepting the monophyly of *Balizoma* and the "obtusa group" sensu Ramsköld (1986a), a condition (e.g., tall genal field) shared by *B. variolaris* and primitive parts of the "obtusa group" is observed in a doublet of terminal taxa (sensu Maddison et al., 1984) and is parsimoniously inferred to be the plesiomorphic state for the genus. It is observed that American Ludlow species allied to *B. obtusa* also have taller genal fields (90–95% height of border) than Baltic material [e.g., *B. indianensis* (Kindle and Breger, 1904), Milwaukee Public Museum 26014, reefal Racine Dolomite, Thornton, Illinois; *Balizoma* n. sp., Yale Peabody Museum 16270, Brownsport Formation, near Decaturville, Tennessee].

Outgroup comparison with inferred primitive states for *Balizoma* and the Llandovery "Nucleurus" grade suggests that these similarities are apomorphic. This hypothesis of unique common ancestry of *Mackenziurus* and *Fragiscutum* (i.e., sister-group relationship) identifies Laurentia as an area of ende-

mism, and the two genera have similar temporal distributions (see below). Ramsköld (1986a) suggested that *Fragiscutum* may be descended from an early Llandovery branch of the *variolaris* plexus including *Encrinurus rotundus* Männil, 1977. This species shows cephalic features which are generally plesiomorphic for the plexus, and pygidial form (16 axial rings/8 pleural ribs; R/P ratio about 1.8) indeed comparable to *Fragiscutum* (R/P ratio approximately 1.7–2.0). A unique common ancestor of *Mackenziurus* and *Fragiscutum* may thus have differentiated in the early Llandovery. There is, however, an appreciable stratigraphic gap separating the known occurrence of *Mackenziurus* (mid-Wenlock) and *Fragiscutum* (late Wenlock or early Ludlow) from this hypothesized “stem species.” We follow Tripp et al. (1977), Strusz (1980), and Ramsköld (1986a) in restricting *Fragiscutum* to the type species, *F. rhytium* from Maine, and *F. glebale* from Oklahoma (and the Ludlow Brownsport Formation of west central Tennessee; Edgecombe, in prep.). These (late Wenlock?) Ludlow species are distinguished from other *variolaris* plexus taxa by the development of only 10 thoracic segments; low (nonpedunculate), enlarged eyes; and marked adaxial displacement of lateral glabellar lobe tubercles. Figure 3 documents allometric change in length of the palpebral lobe relative to length of the cranium for *Fragiscutum*, *Mackenziurus*, and *Balizoma* species. These data suggest that the large-eyed condition (a synapomorphy of *Fragiscutum*) resulted from accelerated rate of eye size increase (relative to the primitive small-eyed state of *Balizoma* and *Mackenziurus*; it is noted that some Ludlow species of *Balizoma* have enlarged eyes; see discussion below). The taxonomic significance of the reduced number of thoracic segments in *F. rhytium* and *F. glebale* has been questioned (Perry and Chatterton, 1979; Holloway, 1980). However, since the plesiomorphic state of 11 segments is so fixed and widespread within Encrinurinae, the uniquely shared state in this character (in congruence with the others listed above) provides a reliable synapomorphy. Reports of *Fragiscutum* from Greenland (Lane, 1984) and Arctic Canada (Perry and Chatterton, 1977; Pojeta and Norford, 1987) are here recognized as *Balizoma*. As now

known, *Fragiscutum* is an eastern/southern Laurentian endemic.

Mackenziurus n. gen. may be most readily distinguished from *Fragiscutum* by its lower number of pygidial pleural ribs and, particularly, axial rings, with a resultant low R/P ratio (1.1–1.3 versus 1.7–2.0). In this character, *Fragiscutum* more closely resembles the primitive condition in “*Nucleurus*” (while *Mackenziurus* is similar to *Balizoma*, as discussed below).

The type species, *M. reimeri* n. sp., reveals distinctive autapomorphies differing from those of *Fragiscutum*:

1. Almost complete reduction of the hypostomal rhychos, and associated (as coaptative structures) absence of a U-shaped posteromedian notch in the inner margin of the pygidial doublure. Holloway (1980) observed that this notch, permitting insertion of the rhynchos into the pygidial doublure during enrollment, is well developed in species here assigned to *Balizoma* and *Fragiscutum*, while Edgecombe and Chatterton (1987) further suggested a correspondence between these coaptative structures and the plesiomorphic encrinurine enrollment pattern. Despite modification (i.e., almost complete loss) of both of these structures in *Mackenziurus reimeri*, the shallow vincular furrow and distinct marginal flange beneath the anterior three or four pygidial pleural ribs are comparable to those of *Fragiscutum* and *Balizoma*, and suggest similar cephalic-pygidial interlocking mechanisms. *Mackenziurus* sp. (Tripp et al.) retains a broad, shallow posteromedian notch, comparable to that of *Fragiscutum glebale*.

2. Broader (tr.) rostral plate (possibly an allometric byproduct of broadening the frontal glabellar lobe). In this character, *Mackenziurus reimeri* most closely resembles Ludlow *Frammia* (see cephalon of *F. arctica* figured by Tripp et al., 1977: pl. 115, fig. 16; text-fig. 4). The rostral plate of *F. arctica* differs from that of *M. reimeri*, however, in narrowing ventrally, instead of being subrectangular. Broadening of the rostral plate is regarded as a convergence between these taxa; a greater number of putative synapomorphies suggest that *Frammia* shares unique history with part of “*Nucleurus*,” such as *E. (“N”). elegantula* (Billings, 1866) (and pos-

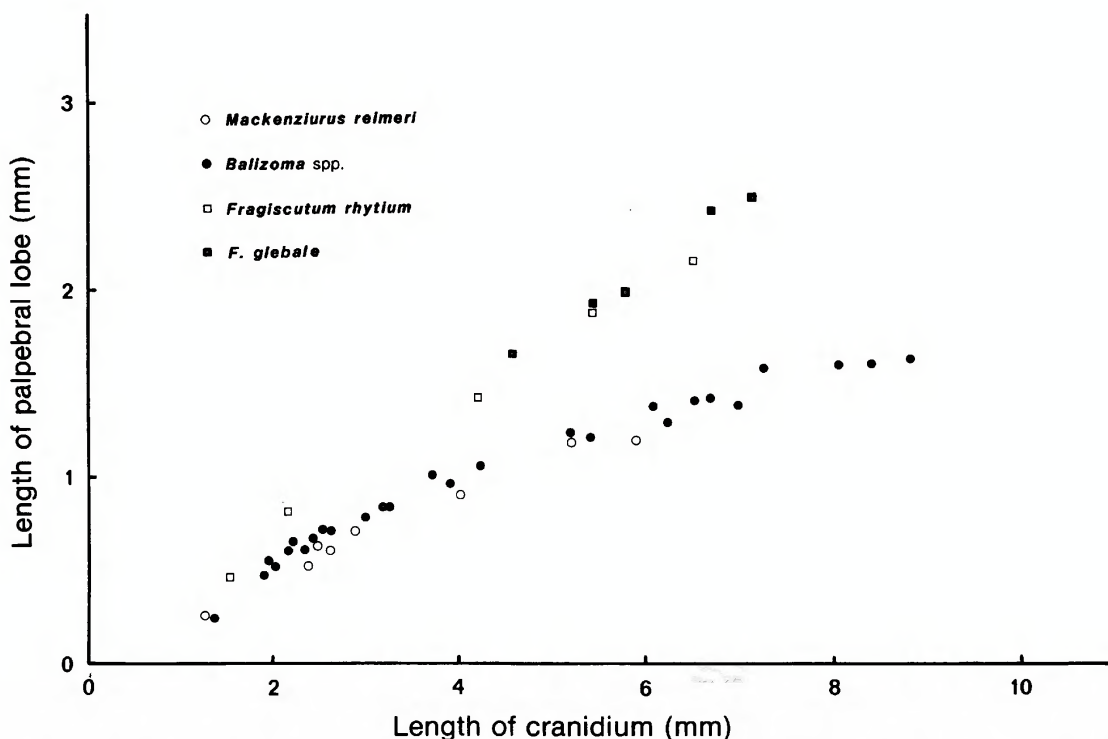


Fig. 3. Scatter plot of maximum length of palpebral lobe versus sagittal length of cranium in taxa of the *variolaris* plexus. Data for *Fragiscutum rhytium* and *F. glebale* from photographs in Whittington and Campbell (1967) and Campbell (1967), respectively; additional specimens of *F. glebale* measured are Milwaukee Public Museum 26523 (Henryhouse Formation, Oklahoma) and Yale Peabody Museum 16271 (Brownsport Formation, near Decaturville, Tennessee). *Mackenziurus reimeri* from section Avalanche Lake Five, 58–60 m above base, and section Avalanche Lake Seven, 27 m above base. *Balizoma* spp. from section Avalanche Lake Four, 126 m above base [= *Balizoma dimitrovi* (Perry and Chatterton, 1979) of Edgecombe and Chatterton, 1987: fig. 7].

sibly *E. globosus* Maksimova, 1962), and also primitively had a narrower rostral plate. Characters supporting this grouping include a rounded genal angle, short and wide glabella, lateral lobe tuberculation much enlarged relative to low, dense glabellar tubercles, strong reduction of L1 dorsally, and reduction/loss of pygidial sagittal tuberculation. The (primitive) presence of a typical narrow rostral plate in *Mackenziurus* sp. (Tripp et al., 1977), which shares several apomorphic characters with *M. reimeri*, suggests that broadening of the rostral plate occurred independently within *Frammia* and *Mackenziurus*.

3. Modification of the adaxial fixigenal tubercle row, with two coarse tubercles overhanging the axial furrow opposite S1 and S2 in largest holaspides (figs. 6: 8; 7: 1). Consid-

ering the outgroups *Pacificurus* and *Encrinurus*, five adaxial fixigenal tubercles would appear to be plesiomorphic for the *variolaris* plexus; species of “*Nucleurus*” have three to five, and *Balizoma* usually has five or six. Species of *Mackenziurus* and *Fragiscutum* develop two (some *M. reimeri*), three (some *M. reimeri*; *F. glebale*), or four (*Mackenziurus* sp. of Tripp et al.) tubercles in the adaxial fixigenal row. *F. rhytium* is more variable, with holaspides having three, four, or (rarely) five adaxial fixigenal tubercles. Growth series for *Balizoma* spp. and *Mackenziurus reimeri* indicate that development of this row is initiated in the meraspid period (fig. 4), although clusters of tiny spinose denticles along the axial furrow opposite S1 and S2 in early meraspides are a precursor to tubercle development. Edgecombe and Chatterton (1987)

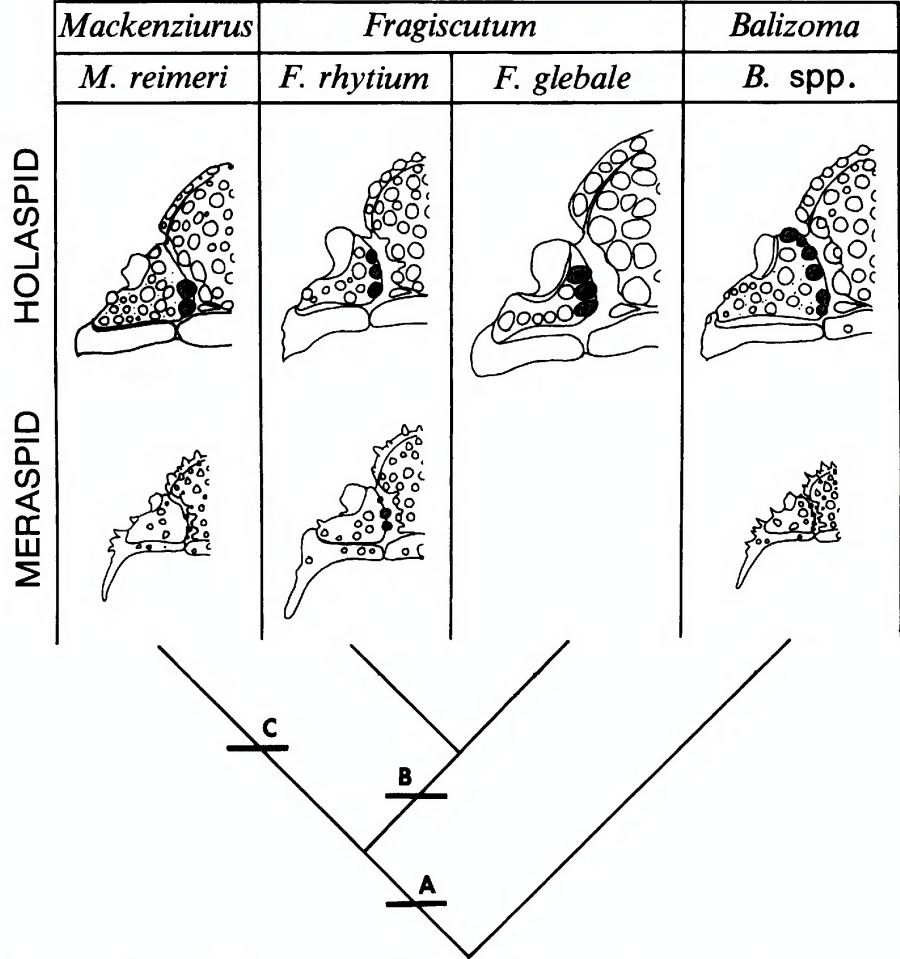


Fig. 4. Comparative ontogeny of the genal field and phylogenetic relationships in the *variolaris* plexus. Adaxial fixigenal tubercles in meraspides (bottom row, approximately $\times 11$) and large holaspides (top row, approximately $\times 5.5$) are shaded. Apomorphic character transformations: A. reduction of adaxial fixigenal row to 2–4 (rarely 5) tubercles; B. enlargement of eyes (accelerated rate of allometric growth); C. adaxial row in large holaspides dominated by coarse tubercles opposite S1–S2. Based on originals of figs. 6: 8, 7: 1, and 8: 5 (*Mackenziurus reimeri*); Whittington and Campbell, 1967: pl. 12, figs. 1, 15 (*Fragiscutum rhytium*); Campbell, 1967: pl. 8, fig. 8 (*F. glebale*); Edgecombe and Chatterton, 1987, fig. 6G and unpublished (*Balizoma* spp. cf. *B. dimitrovi*).

noted that this tubercle row in *Balizoma* formed as a unified series distinct from other genal tubercles in Ramsköld's (1986a) "circumocular tubercle ring." *Balizoma* meraspides show a rather uniform-size row of small, granulose tubercles opposite the glabellar furrows (and farther forward opposite the abaxial end of the preglabellar furrow), although earlier onset of development results in slightly larger tubercles opposite S1 and S2. This adaxial fixigenal row enlarges through ontogeny relative to other fixigenal tubercles, and

is composed of five or six (rarely seven) sub-equal-size tubercles in adults. Apomorphy "A" in figure 4 is conditional upon a second outgroup having five or more adaxial fixigenal tubercles; this applies to "*Nucleurus*" *rotundus* (Männil, 1977), which Ramsköld (1986a) suggested was near the ancestry of *Balizoma* and *Fragiscutum*. However, it would be more parsimonious that *Balizoma* is autapomorphic using four-tubercle "*Nucleurus*" as second outgroup.

In contrast to the inferred plesiomorphic

state, a reduced number of adaxial fixigenal tubercles in *Fragiscutum* and *Mackenziurus* is expressed in the meraspid period by prominence of tubercle pairs opposite S1–S2, but tubercles opposite S3 being either absent (in *M. reimeri*) or small (in *F. rhytium*). This includes meraspides at degrees certainly more advanced than those at which *Balizoma* has developed five tubercles in the row (see fig. 4). Further development of the adaxial row is often completely arrested in *Mackenziurus reimeri*, in which tubercles opposite S1 and S2 coarsely enlarge through the growth series, but anterior or posterior pairs are usually either small or absent in large holaspides. This pedomorphic state differs from the more primitive condition of *F. rhytium*, in which a row of three to five subequal-size tubercles also includes pairs positioned opposite S3, and sometimes opposite the prelabellar and/or occipital furrows, more comparable to “*Nucleurus*” and *Balizoma*. Holaspides of *Fragiscutum glebale* Campbell, 1967, have three nodular tubercles opposite S1–S3. A correlation is apparent between expansion of the greatly enlarged eyes to immediately adjacent to the axial furrow and reduction in the area of the genal fields and reduced adaxial fixigenal tuberculation (i.e., absence of anterior tubercles sometimes developed in *F. rhytium*). It is thus plausible that accelerated rate of eye size increase (fig. 3) imposed a spatial constraint on ontogenetic development of late-forming anterior tubercles in the adaxial fixigenal row.

Mackenziurus may also be distinguished from *Fragiscutum* by its primitive character states of smaller eyes on short eye socles, symplesiomorphies with Llandovery “*Nucleurus*.” These states are also retained in Wenlock species of *Balizoma*, such as the type species, *B. variolaris* (Brongniart). They are apparently plesiomorphic conditions for the group of species allied to *B. obtusa* (Angelin) [see fig. 3 for eye size of Wenlock *B.* spp. cf. *B. dimitrovi*; see Perry and Chatterton, 1977: pl. 4, fig. 26; 1979: pl. 74, fig. 21, for eye socle]. The large, sessile eyes of some Ludlow “*obtusa* group” species (e.g., *B. obtusa* Form B of Ramsköld, 1986a) are thus inferred to be homoplastic with *Fragiscutum*. The number of thoracic segments in the new

genus is unknown. There is a possibility that reduction in the number of thoracic segments to 10 originated in a common ancestor of the *Mackenziurus*–*Fragiscutum* clade.

Species here referred to *Mackenziurus* n. gen. were assigned to *Balizoma* by Holloway (1980) and Ramsköld (1986a). Shared character states are partly plesiomorphic for the *variolaris* plexus (or perhaps a *Mackenziurus*–*Fragiscutum*–*Balizoma* clade), and reflect descent of both genera from Llandovery lineages grouped as “*Nucleurus*.” It is recognized that *Mackenziurus* shows greater similarity in its low R/P pygidial form to *Balizoma* (notably *B. variolaris*) than to *Fragiscutum* (e.g., see Schrank, 1972: pl. 13, fig. 8; Tripp et al., 1977: pl. 113; Thomas, 1981: pl. 18, fig. 2). As well, both taxa typically bear sagittal tubercles on every second axial ring. However, as Ramsköld (1986a) noted, sagittal tubercle spacing is correlated with the number of axial rings; it is thus not feasible to recognize these as independent similarities. The criterion in postulating *Fragiscutum* as sister group to *Mackenziurus* is parsimony; a greater number of apparent synapomorphies unite these taxa than unite *Mackenziurus* with *Balizoma* (e.g., unique hypostomal characters). The similarity of the *Mackenziurus* pygidium to that of *B. variolaris*, however, provides a competing hypothesis to test with additional characters.

Characters by which *Mackenziurus* may be distinguished from *Balizoma* include the following:

1. relatively small size;
2. reduction of the adaxial fixigenal tubercle row to two to four tubercles (versus, typically, five or six subequal-size tubercles in *Balizoma*);
3. subpentagonal hypostome with reduced rhynchos and maculae, and rounding/flattening of the middle body (versus rhomboid hypostomal outline, prominent rhynchos and maculae, and inflated, subovate middle body in *Balizoma*). Maculae are bulbous in *B. variolaris* (Tripp et al., 1977: pl. 113, figs. 5, 10); they are distinct in Wenlock *B. dimitrovi*? (Perry and Chatterton, 1977: pl. 4, fig. 8) and Ludlow *B. dakon* Šnajdr, 1983 (Šnajdr, 1985: pl. 12, fig. 9), *B. rosensteinae* (Tripp et al., 1977: pl. 115, fig. 4), and *B. obtusa* (Schrank,

1972: pl. 11, fig. 8a). As suggested above, some of these differentia may be restricted to *M. reimeri*;

4. a low, more sparsely tuberculate librigenal field (typically bearing two "rows" of tubercles in *Balizoma*);

5. more round-margined pygidium, usually with fewer axial rings and pleural ribs (7–9 rings in *Mackenziurus* n. gen. versus 9–11 in *Balizoma variolaris*, 10–15 in *B. obtusa* and allied species; 6–8 ribs in *Mackenziurus* versus 7–8 in *B. variolaris*, 8–12 in *B. obtusa* and allied species). As a result, the pygidial R/P ratio is typically lower (see Ramsköld, 1986a: text-fig. 3); and,

6. posteromedian notch in inner margin of pygidial doublure is shallower or absent.

The recognition of *Mackenziurus* n. gen. thus restricts the degree of morphological variation within *Balizoma* as diagnosed by Ramsköld (1986a).

West Malaysian late Llandovery or early Wenlock *Langgonia* Kobayashi and Hamada, 1971, shows at least superficial resemblance to *Mackenziurus*. Holloway (1981) convincingly argued that this genus, originally described in a new monotypic subfamily of Dalmanitidae, lacks synapomorphies of the more-inclusive Phacopina and shares unique characters with Encrinuridae. These include a longitudinal median glabellar furrow, straight (tr.) lateral glabellar furrows, short L1–L3, and librigenal precranial lobes; derived characters of Encrinurinae (or subgroups) include a forward-expanding glabella, tuberculiform L2–L3, adaxial fixigenal lobes opposite the lateral glabellar furrows, and more than five aspinose pairs of pygidial pleurae. Its pygidial morphology (e.g., hemispherical shape with seven rib pairs, and seven or eight axial rings) and overall conformation of the librigena (especially in small-eyed *L. araiorachis* Kobayashi and Hamada) are similar to those of *Mackenziurus*. The Malaysian species obviously possess many autapomorphies (e.g., the transverse furrow on the fixigenal field separating the adaxial lobes), but these are uninformative in discerning outgroup affinities. Plesiomorphies which would, however, exclude *Langgonia* from the *variolaris* plexus include its well-developed L1, transverse S1, and absence of

coarse glabellar and pygidial sagittal tuberculation. From the ambiguous evidence currently available, *Langgonia* is regarded as Encrinuridae incertae sedis, with some convergent similarity to Laurentian *Mackenziurus*.

Mackenziurus reimeri n. sp.

Figures 5–8

Types: Holotype pygidium UA 7843 (fig. 6: 14, 16–18), and paratypes UA 7836–7842, 7844–7853, 7857, 7861. Type locality is section Avalanche Lake Five, 58–60 m above base (Delorme Formation, Wenlock; see Over and Chatterton, 1987).

Occurrence: Type locality; Avalanche Lake Four, 136–138 m above base; Avalanche Lake Seven, basal 70 m of measured section (occurrences at AV7-0, 27, 38, and 70 m above base).

Diagnosis: Species of *Mackenziurus* with L1 present as low, discontinuous lobes; maximum glabellar convexity forward on frontal lobe, which bears small paired lateral lobe tubercles; I-1 present; genal spines bluntly pointed; axial furrow diverges abruptly in front of enlarged fixigenal tubercle pair opposite S2. Librigenal field bears several smaller adventitious tubercles in addition to row of 6–7 coarse tubercles. Lateral border tuberculation weak. Rostral plate wide, subrectangular. Eye opposite S3. Pygidial length 55–65 percent of width, with 7–8 pleural ribs, 8–9 (rarely 10) axial rings; axial tuberculation includes alternating small and large sagittal tubercles and paired tubercles abaxial to sagittal groove on several anterior rings; inner margin of pygidial doublure broadly parabolic, lacking posteromedian notch.

Etymology: After Mr. Weldon Reimer of the Canada Tungsten mining operation, Tungsten, Northwest Territories.

Description: Cranial length 55–65 percent of width; L4 140–150 percent of width of L3, and 120–130 percent of width of occipital ring. Glabellar length 110–120 percent of width across L4, with maximum convexity positioned forward on frontal lobe. S1 directed posteromedially and merging with occipital furrow behind I-1 tubercle pair. Lateral lobe L4 bearing a pair of exsagittally

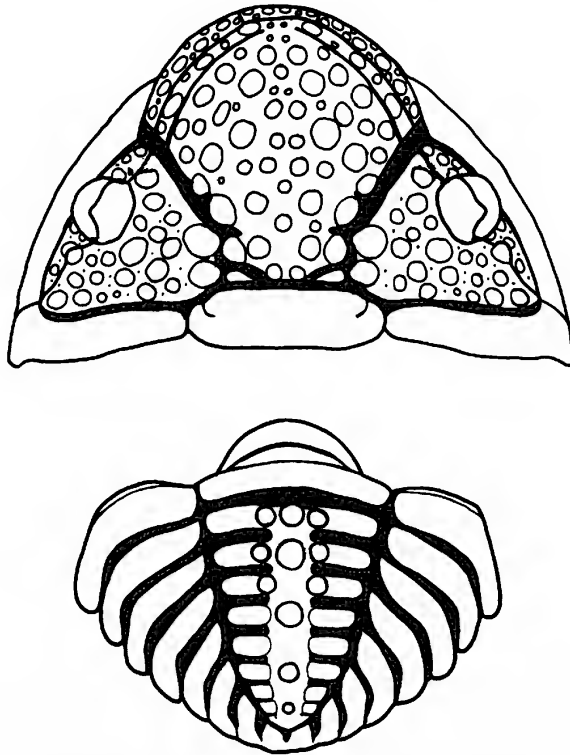
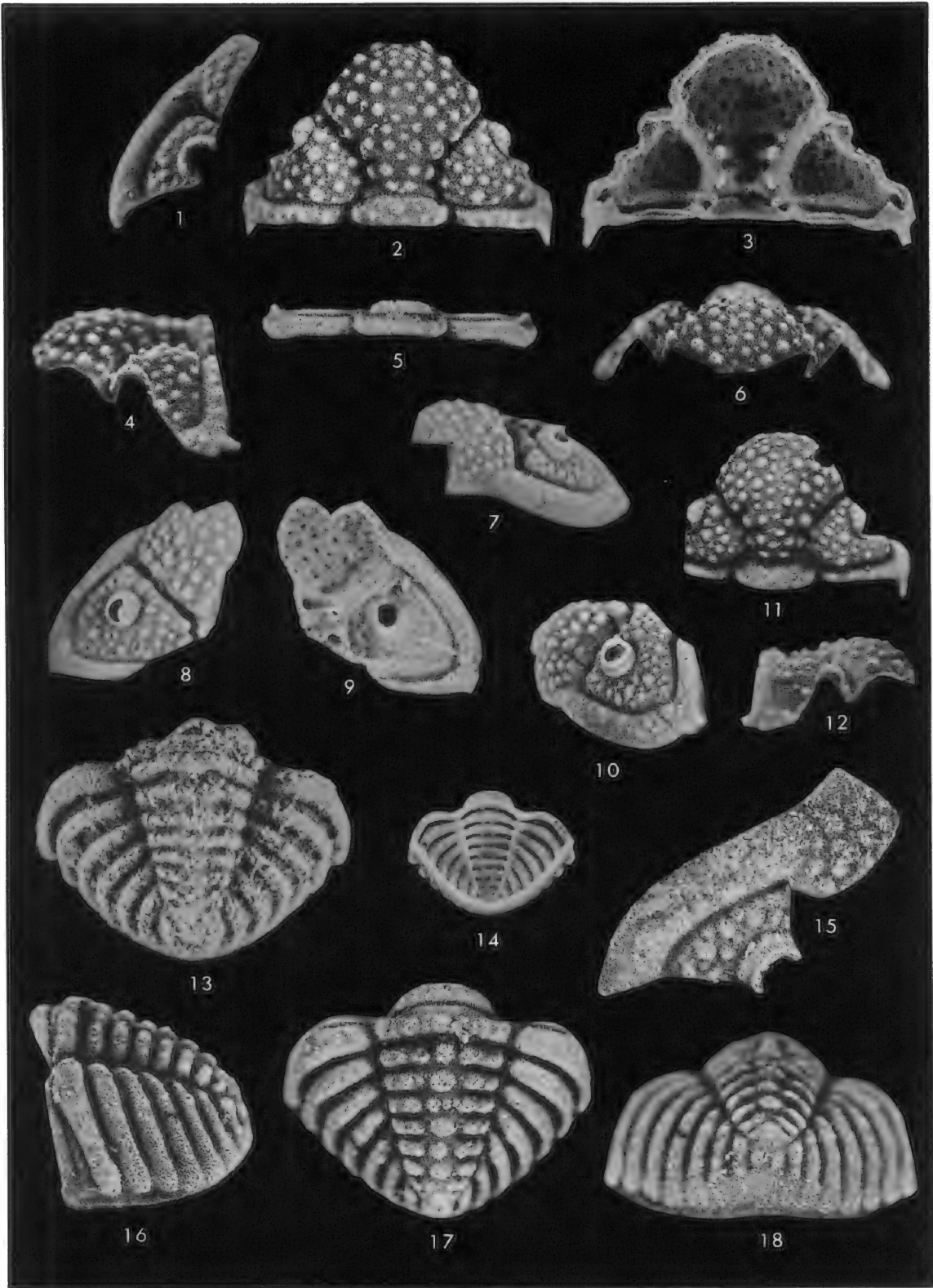


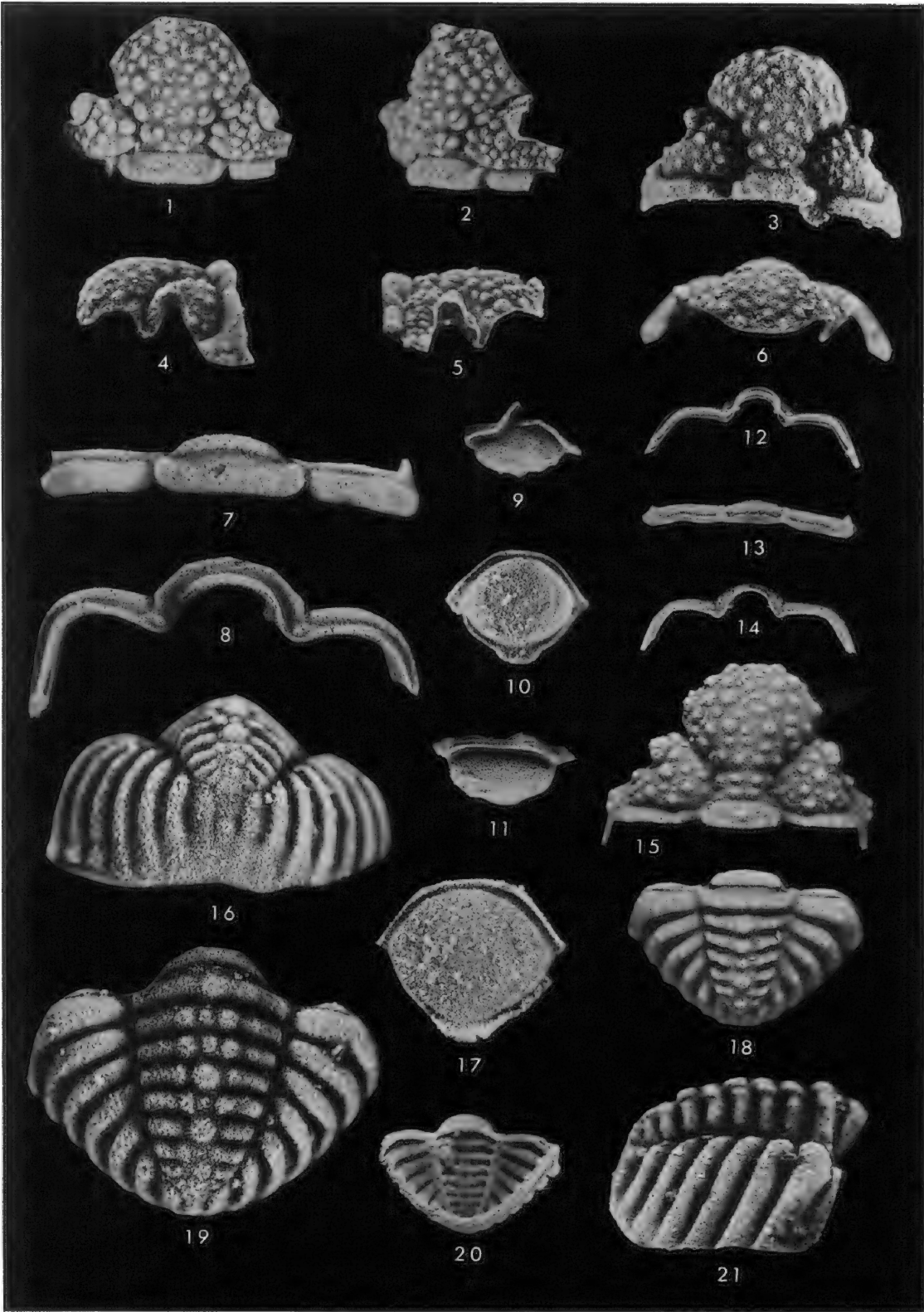
Fig. 5. Dorsal view of a reconstruction of cephalon and pygidium of *Mackenziurus reimeri* n. gen. n. sp.

aligned tubercles (small adaxially positioned anterior tubercle, and larger posterior tubercle), contrasting with single rounded tubercles on L2-L3 distinctly larger than more medial glabellar tubercles. Glabellar tuberculation includes I-1; II-1, 2; iii-0; III-1, 2^F, 3; frontal lobe bears distinct IV-1, 2, 3^{F/R}; V-1, 2; VI-1, and smaller inter-row tubercles. Occipital ring and cranidial posterior/posterolateral border tuberculate in all but largest holaspides (see Ontogeny). Preglabellar furrow shallow; adaxially narrowing anterior border bears 10-14 tubercles, abaxialmost

pair (PL) not relatively enlarged; cranidial anterior margin straight sagittally, defining wide (tr.) rostral suture. Adaxial fixigenal margin almost straight anterior to enlarged subconical tubercles overhanging axial furrow opposite S1-S2. Palpebral lobe with anterior edge close to axial furrow, but separated from it by one small tubercle. Fixigenal field pitted, densely tuberculate, including distinct CT1-CT4 of subequal size to coarsest glabellar tubercles; CT1 adjacent to posterior limit of palpebral lobe (opposite front of L2 to back of L3).

Fig. 6. *Mackenziurus reimeri* n. gen. n. sp., Delorme Formation, Mackenzie Mountains, Northwest Territories, Canada. All specimens from section Avalanche Lake Five, 58-60 m above base (Over and Chatterton, 1987) except 13 (from section Avalanche Lake Four, 138 m above base), $\times 10$ except where noted otherwise. 1. UA 7836, dorsal view of librigena. 2-4, 6. UA 7837, dorsal, ventral, lateral, and anterior views of cranidium. 5. UA 7838, dorsal view of thoracic segment. 7-10. UA 7839, anterior, dorsal, ventral, and lateral views of incomplete cranidium and librigena. 11. UA 7840, dorsal view of cranidium. 12. UA 7841, lateral view of cranidium. 13. USA 7842, dorsal view of pygidium. 14, 16-18. UA 7843, ventral ($\times 5$), lateral, dorsal, and posterior views of holotype pygidium. 15. UA 7844, external view of librigena.





Librigenal field pitted; height (tr.) about 70 percent of lateral border, very slightly longer (exsag.) than densely tuberculate precranial lobe. Anterior furrow shallow. Eye socle about 60 percent as high as visual surface, defined by distinctly incised furrows.

Cephalic apodemes expanded distally, directed inward at outer end of occipital furrow, S1, S2, and S3; S1-S2 apodemes large, longitudinally ovate and subspherical respectively; occipital and particularly S3 apodemes small. In ventral view, S3 short, anteromedially directed; straight S2 weak but distinct across much of glabella. Cephalic doublure uniformly broad beneath librigenal lateral border but narrowing gently beneath anterior border – precranial lobe; cranial doublure narrows abruptly adaxial to genal angle. Shallow vincular furrow along ventrolateral margin of librigenal doublure corresponding with marginal flange beneath anterior three or four pairs of pygidial pleural ribs. Pygidial doublure broad, widening slightly posteromedially.

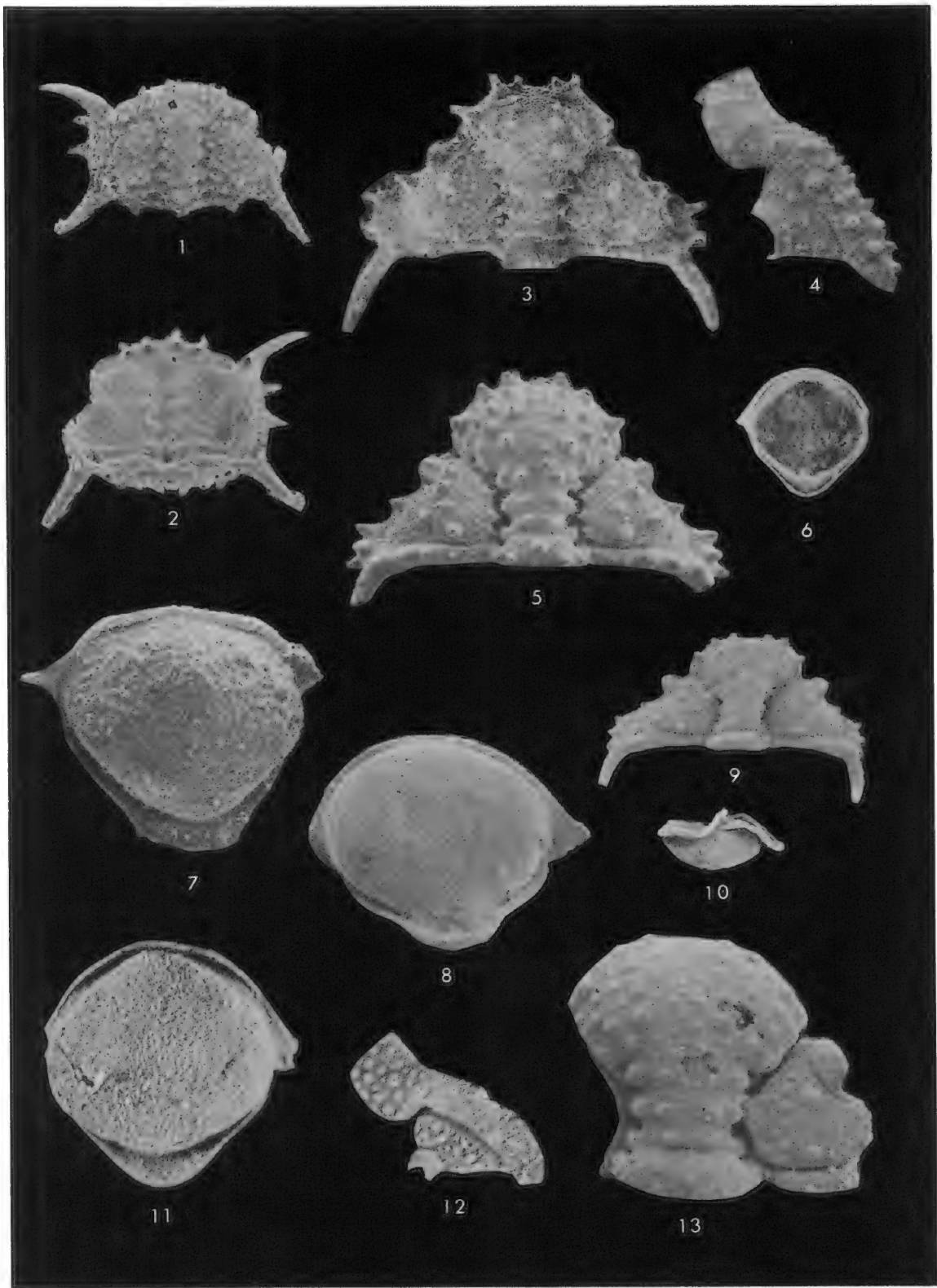
Rostral plate (shape inferred from course of rostral, connective, and hypostomal sutures, and from specimens with complete librigenae articulated with cranidium) subrectangular, narrowing very slightly ventrally, width (tr.) approximately 150 percent of sagittal length.

Hypostome with large middle body, slightly broader than long, overhanging lateral border behind anterior wing. Rhynchos weakly developed as faint swelling on anterior margin of middle body, defined abaxially by very shallow, strongly posteriorly divergent furrows, and incorporating about 60 percent of width of middle body opposite front of anterior wings. Maculae forming small, very low, ovate swellings on posterolateral margin of middle body. Anterior border uniformly nar-

row and weakly flexed downward; anterior border furrow rather broad, shallow, and with elongate pits anterolaterally at change in curvature of margin; anterior margin rather straight sagittally, with abrupt posterolateral reorientation on straight anterolateral margins so that outline of hypostome is subpentagonal (particularly in small growth stages). Anterior wing large, positioned anterior to midlength of middle body, shorter in height than middle body, and with short wing process near upturned anterior edge. Posterior wing positioned almost midway between anterior wing and posterior margin of middle body. Doublure narrow, but widening slightly posteriorly and extending almost halfway to posterior border furrow, inner margin lacking anteriorly projecting posteromedian tongue (as present in *Fragiscutum rhytium* and many other encrinurines). Posterolateral border narrow, widening gradually posteromedially; border furrow deep, narrow, and shallowing sagittally. Margin flexed backward posterolaterally with distinct lengthening of broadly rounded posterior border, angled ventrally, comprising less than 10 percent of sagittal length of hypostome.

Number of thoracic segments unknown. Axial ring comprising about 35 percent of width of thorax, bowing gently forward medially and adjacent to rather deeply impressed axial furrow; articulating half-ring about 40 percent of sagittal length of axial ring; ring moderately convex, rounded, or weakly flattened sagittally. Inner half of pleurae sloping gently inward and fairly straight, outer half strongly curved downward; pleural band gently widening abaxially toward abrupt change in slope, abaxially narrowing and gently flexing backward with a weakly concave anterior margin; pleurae terminating in a bluntly rounded point. Axial articulating

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Fig. 7. *Mackenziurus reimeri* n. gen. n. sp., Delorme Formation, Mackenzie Mountains, Northwest Territories, Canada. All specimens from section Avalanche Lake Five, 58–60 m above base (Over and Chatterton, 1987) except 3, 4, and 6 (from Avalanche Lake Seven, 27 m above base), $\times 10$ except where noted otherwise. 1, 2, 5. UA 7845, dorsal, dorsolateral, and lateral views of cranidium. 3, 4, 6. UA 7846, dorsal, lateral, and anterior views of cranidium. 7, 8. UA 7847, dorsal, and anterior views of thoracic segment. 9–11. UA 7848, lateral, ventral, and anterior views of hypostome. 12–14. UA 7849, anterior, ventral, and posterior views of thoracic segment, $\times 5$. 15. UA 7850, dorsal view of cranidium. 16, 19–21. UA 7851, posterior, dorsal, ventral ($\times 5$), and lateral views of pygidium. 17. UA 7852, ventral view of hypostome. 18. UA 7853, dorsal view of pygidium.



processes prominent, transversely ovate; anterior articulating flange uniformly narrow and about 30 percent length of pleural band in inner half of pleurae, widening abaxially and projecting forward abaxial to fulcrum to form a prominent bluntly pointed facet. Doublure of axial ring gently widening sagittally to almost 50 percent of length of segment; apodemes positioned slightly inward of axial furrow, directed strongly inward and weakly downward; posterior recess well developed in inner half of pleural doublure.

Downturned outer part of the first pair of pygidial pleural ribs inclined at 70–80°; interrib furrows widened toward change in slope, then narrow distally at expanded tips of pleural ribs; posterior two or three pairs of interrib furrows indistinctly continuous to ventral margin of pygidium (distal part of pleural ribs fused). All but the anterior one or two axial rings with a narrow sagittal groove; in lateral view, axis is gently convex and weakly sloping for most of length but with abrupt steep slope posteriorly.

DISCUSSION: *Mackenziurus reimeri* n. gen. n. sp. can be distinguished from *Mackenziurus* sp. (Tripp et al., 1977), from the Middle Wenlock of Illinois and Wisconsin, by cephalic characters listed in the species diagnosis above. Also, the new species has a taller, more strongly sloping pygidial profile, lacking a posteromedian notch in the doublure.

Mackenziurus pygidia from the St. Clair Limestone of Arkansas described by Holloway (1980) as *Balizoma* sp. are more elongate and slope more strongly in lateral view (notably postaxially) than those of *M. reimeri* n. sp. The Arkansas species has only six pleural ribs that are more strongly turned downward and backward abaxially, the first rib being almost vertically inclined; seven axial rings; and a shallower sagittal groove. Holloway at-

tributed the small number of axial rings and pleural ribs to the small size of known specimens, apparently implying that these were juveniles. This possibility is somewhat weakened by comparison with similarly small adult holaspides of *M. reimeri*, in which a full complement of eight pairs of pleural ribs may be attained in pygidia of length as little as 25 percent of the largest known specimens, and by the ontogenetically advanced appearance of the smooth pygidial margin (lacking spinose rib terminations characteristic of early ontogeny in the type species and other taxa of the *variolaris* plexus).

ONTOGENY

Silicified material of *Mackenziurus reimeri* n. gen. n. sp. includes a relatively complete growth series for most sclerites, recording ontogenetic development from the protaspis through holaspis periods.

A protaspis of this species figured by Edgecombe et al. (1988) as "*Balizoma* sp." [*variolaris* plexus n. gen. n. sp.] is reillustrated herein (fig. 8: 1, 2) to document ontogenetic changes across the protaspis–meraspis transition. Trends in postprotaspis ontogeny are generally comparable to those documented by Whittington and Campbell (1967) in *Fragiscutum* and by Edgecombe and Chatterton (1987) in *Balizoma*. These include the following:

1. Near isometry in glabellar length/width (fig. 9A) and width of the frontal lobe relative to L1–L3 (fig. 9B); slight increase in both ratios with increasing size. Protaspis with subovate frontal lobe, slightly broader than subequal (in length and width) L2–L3, with straight, transglabellar S1–S3. Growth series demonstrating relative lengthening of frontal lobe, becoming subhemispherical in outline,

Fig. 8. *Mackenziurus reimeri* n. gen. n. sp., Delorme Formation, Mackenzie Mountains, Northwest Territories, Canada. All specimens from section Avalanche Lake Five, 58–60 m above base (Over and Chatterton, 1987) except 6, 10, and 11 (from section Avalanche Lake Four, 138 m above base). All figures except 6 and 10–12 are scanning electron micrographs. 1, 2. UA 7829, dorsal and ventral views of protaspis, $\times 75$. 3. UA 7854, dorsal view of small (meraspis) cranidium, $\times 50$. 4. UA 7855, external view of small librigena, $\times 50$. 5. UA 7856, dorsal view of small cranidium, $\times 30$. 6, 10, 11. UA 7857, dorsal, lateral (both $\times 5$), and ventral ($\times 10$) views of hypostome. 7. UA 7858, ventral view of small hypostome, $\times 50$. 8. UA 7859, ventral view of hypostome, $\times 30$. 9. UA 7860, dorsal view of small cranidium, $\times 30$. 12. UA 7861, external view of librigena, $\times 5$. 13. UA 7862, dorsal view of small cranidium, $\times 30$.

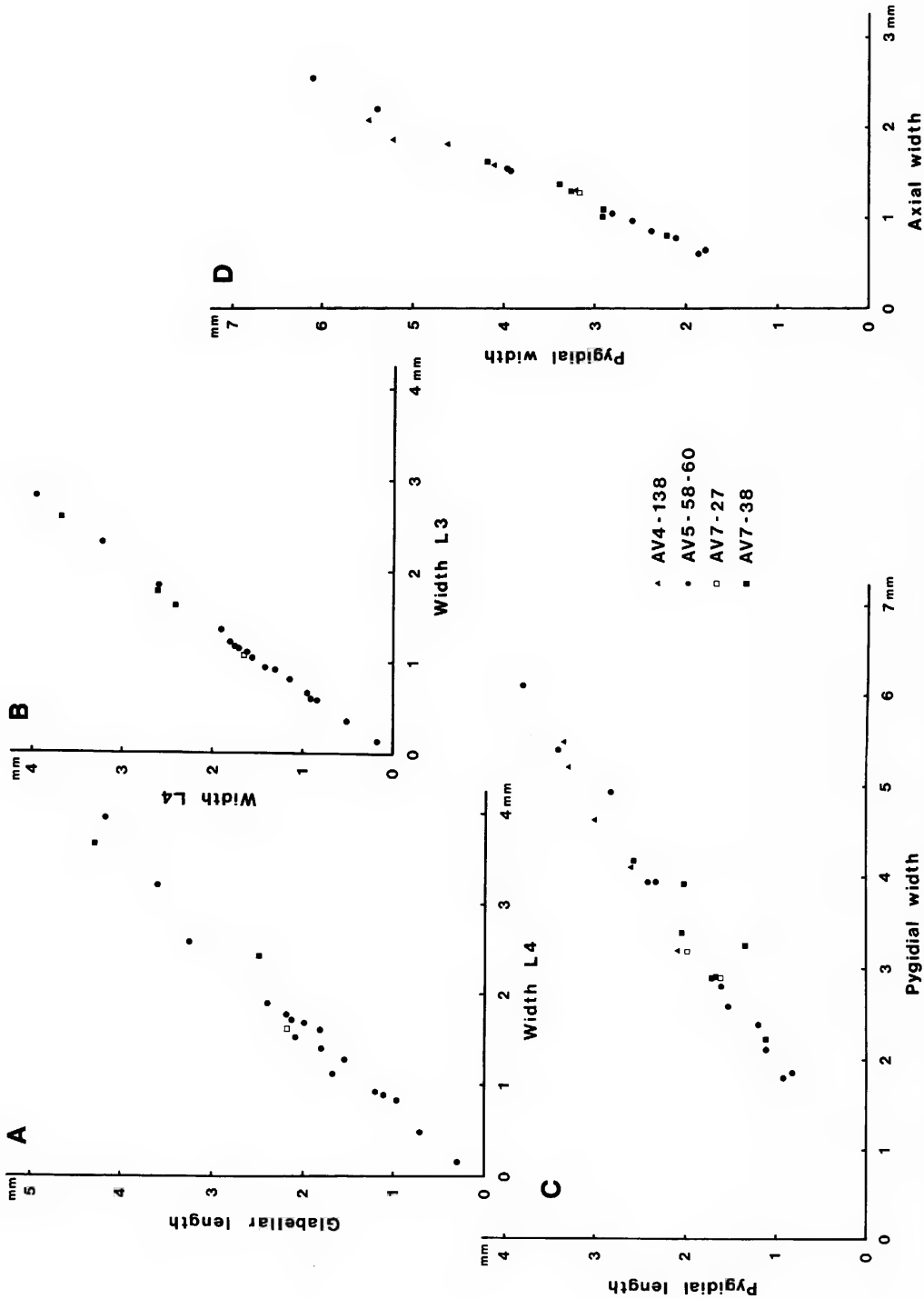


Fig. 9. Bivariate scatter plots of glabellar and pygidial growth for *Mackenziurus reimeri* n. gen. n. sp. from section Avalanche Lake (AV) Four, 138 m above base; AV Five, 58-60 m above base; AV Seven, 27 and 38 m above base (Over and Chatterton, 1987). A. Glabellar length (sag.) versus width across L4 for 20 specimens (protaspid through holaspid period). B. Glabellar width across L4 versus width across L3 for 21 specimens. C. Pygidial length versus width for 25 holaspides. D. Pygidial width versus axial width for 22 holaspides.

with S3 reduced to short anteromedially oriented furrow; S2 remaining straight, but becoming shallow adaxially, S1 reorienting posteromedially to merge with occipital furrow behind I-1 tubercle pair; L1 greatly reduced to low, discontinuous lobes in large holaspides (fig. 7: 1, 2), although continuous L1/straight S1 sometimes retained into holaspid period (fig. 6: 2).

2. Glabellar tubercle development typical for the *variolaris* plexus, as documented for *Balizoma* by Edgecombe and Chatterton (1987). Protaspis with IV-1 tubercle pair positioned posterolaterally on the frontal lobe; V-1 is present in early meraspides. A small (meraspid) cranium (fig. 8: 3) showing distinct I-1; II-1; III-1; IV-1 (enlarged); V-1; VI-1 spine pairs. At this developmental stage, lateral glabellar lobes nontuberculate (bearing short spines), and inter-row tubercles indistinct. Additional major row tubercles added abaxially through the meraspid period, on L3 (III-2) and frontal lobe (IV-2; V-2). Small inter-row tubercles including iii-0 (and occasionally ii-0), and abundant on frontal lobe. Rounded tubercles developing on L2-L4 lateral lobes, finely denticulate in earlier stages. Large holaspides recording flattening of tubercles through this period (spinose in small growth stages), enlargement of tubercles on L2-L3 lateral lobes relative to more medial tubercles, and allometric trend toward subequal size of major row pairs (IV-1 notably larger in early stages), and enlargement of inter-row tubercles.

3. Occipital ring and cranial posterior/posterolateral border prominently tuberculate in meraspides and small holaspides, but smooth or only faintly tuberculate in large holaspides. Occipital tuberculation including large median tubercle and smaller pair posterolaterally. Occipital ring in large holaspides (fig. 7: 1, 2) broad and conspicuously furrowed; broad, shallow furrow curving posterolaterally from abaxial edge of anterior margin and extending straight across mid-length of occipital ring, separating slightly depressed anterior band from raised posterior/posterolateral band. Longitudinal swellings on abaxial part of occipital ring are comparably developed adjacent to axial furrows on thoracic segments. Such transverse furrowing of occipital ring and swelling of anterolateral

part of thoracic axial rings are weakly developed in other taxa of the *variolaris* plexus, most prominently in *Frammia*. In the type species, *F. arctica* (Salter, 1852; see Bolton, 1965), depressed anterior band very distinctly separated from elevated posterior band and, as noted by Tripp et al. (1977), simulating L1 [cf. Gass and Mikulic's (1982) description of L1 fused to occipital ring].

4. Ten to fourteen tubercles developing on cranial anterior border. Protaspis has two blunt spine pairs (fig. 8: 1, 2); these are elongate spines in small meraspides (fig. 8: 3), with small third pair developing sagittally. Smaller tubercles inserting between these pairs increasing in relative size through the holaspid period, resulting in more uniformly sized row of flattened tubercles in adults.

5. Stout, elongate anterior fixigenal spine of protaspis (subequally long as the posterior fixigenal spine) greatly reduced in early meraspides, and forming rounded CT4 tubercle in holaspides. Midfixigenal spine also reduced, migrating posteriorly in front of posterior fixigenal spine. Posterior fixigenal spine remaining elongate in meraspides, reorienting backward; progressive reduction occurring through holaspid period, with genal angle in large individuals only bluntly pointed.

6. Small, spinose fixigenal tubercles developing along axial furrow opposite S1 and S2 (with clusters of tiny denticles in these positions in early growth stages; fig. 8: 3, 5), coarsening through the growth series, assuming subconical shape, nearly buttressing axial furrow (fig. 7: 1).

7. Small crania demonstrate primary development of CT1/CT2/CT3 fixigenal "circumocular" spines, with torulus becoming indistinct in early meraspides. Fixigenal field undergoing increased tuberculation; later-forming tubercles enlarging to size only slightly smaller than primary "circumocular" tubercles.

8. Palpebral lobe, bearing short spines in early stages, migrating backward from position opposite L4 through much of growth series to opposite S3 in large holaspides.

9. Hypostomal middle body (widest anterolaterally in small stages and more bluntly rounded anteriorly than posteriorly) flattening, becoming rounder in outline, and inflating laterally to overhang lateral border. Small

pair of denticles on lateral border and two pairs on posterolateral border present only in early growth stages (fig. 8: 7).

10. Libriginal lateral border bearing numerous short spines in small stages (fig. 8: 4), reducing to faintly tuberculate adult state. Tuberculation on lateral border preceding that on precranial lobe and field, more densely tuberculate in later ontogeny.

11. Approximately rectilinear increase in pygidial length/width occurring through holaspid period (fig. 9C). Other trends through this period (early holaspides already possessing seven or eight pairs of pleural ribs and eight or nine axial rings) include the following: reduced spinosity of free rib terminations, with smoothing of pygidial margin; deepening and broadening of sagittal groove; shortening of sagittal spines to rounded tubercles, and development of axial tubercle pairs lateral to sagittal groove; loss of pleural tubercles; deepening and broadening of axial and interrib furrows; and, steepening slope of distal part of pleurae. Change in axial width relative to pygidial width nearly isometric (fig. 9D).

ENVIRONMENT AND ECOLOGY

Variable stratigraphic occurrence of *Mackenziurus reimeri* in sections representing a shelf-to-basinward depth gradient in the Avalanche Lake area (see Over and Chatterton, 1987) demonstrates facies control on the distribution of this species. *M. reimeri* occurs through 70 m of thinly bedded, dark gray, argillaceous micrite in Avalanche Lake Seven, the most distal sampled section. This species is represented through progressively narrower stratigraphic intervals in equivalent horizons in shelfward (i.e., shallower) sections. It ranges through only 4 m in section Avalanche Lake Five (thinly bedded micrite underlying a transgressive graptolitic shale), through 2 m in Avalanche Lake Four (dark-colored micrites with coarse bioclastic allochthonous interbeds), and is unrepresented in more proximal Avalanche Lake One and Two. The restricted spatiotemporal distribution and lithofacies association of *M. reimeri* attest to relatively deep-water ecology of constituent organisms, in outer shelf/slope muds. This provides a contrast with occur-

rences of congenierics in other geographic areas; *Mackenziurus* sp. from Illinois and Wisconsin, for example, is known from interreef dolomites. These ecological differences might have been significant in effecting the spatial differentiation of *Mackenziurus*. Further, they attest to the inherent limits in construing taxa (genealogical entities) as coherent ecological entities (cf. Eldredge, 1989). The facies distribution of *Balizoma* species provides a similar example. *Balizoma* cf. *B. dimitrovi* (Perry and Chatterton, 1979) is abundant in sympatry with *Mackenziurus reimeri*. Ramsköld (1985), however, observed the morphologically similar *B. obtusa* (Angelin, 1851) from Gotland to be associated with high-energy reefal calcarenite facies. This emphasizes that differing ecologies are not necessarily correlated with notable phenotypic differences [indeed, Ramsköld (1986a) discussed the problem of separating *B. dimitrovi* from *B. obtusa* on morphological grounds].

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